



# PINNOTHERES OSTREUM, PARASITIC ON THE AMERICAN OYSTER, OSTREA (GRYPHAEA) VIRGINICA<sup>1</sup>

LESLIE A. STAUBER<sup>2</sup>

Oyster Research Laboratory, N. J. Agricultural Experiment Station, Bivalve, N. J.

## INTRODUCTION

The oyster crab, *Pinnotheres ostreum*, was first described by Say in 1817. It is an organism known for many years to oystermen and biologists alike although its habits and life history are but imperfectly known. In her monograph on the grapsoid crabs Rathbun in 1917 defined the adult characters of the genus and compared the numerous species which had been collected from many parts of the world in association with various mollusca, tunicates, annelids and sea urchins. This association has regularly been considered commensalism by most investigators. In the case of *P. ostreum*, however, the relationship is not clear for in 1892, Bashford Dean wrote that the crab was evidently annoying to the oyster for the palps sometimes show thickened out-growths or are malformed and stunted in size. Orton, in 1921, presented clear evidence in the case of the pea crab, *P. pisum*, from the mantle cavity of the mussel, *Mytilus edulis*, that the activity of the crab was definitely parasitic in nature. Ryder, on the other hand, supposed that the crab was of value to the oyster since the latter was said to feed on the clusters of bell-animalcules (*Zoothamnium* sp.) which are attached to the crab's shell. A consideration of the crab's stomach contents, however, showed that its food consists in great part of the minute organisms sought by the host in addition to small crustaceans not normally the oyster's prey.

A sudden increase in the numbers of *P. ostreum* in Delaware Bay in 1941 associated with definite erosions of the gills of the oyster and producing, or at least contributing to, the death of many oysters stimulated a re-examination of the crab. The data obtained (abstracted recently, Stauber, 1942) are the subject of this paper.

## LIFE HISTORY

Atkins (1926) has described the post-planktonic stages in the developmental cycle of *P. pisum* from *Mytilus edulis* in British waters. The situation with *P. ostreum* is so similar that, except for morphological details, it seems to be the same. The invasive stages of the oyster crab are small, hard, flat crabs with a carapace 1.4–3.4 mm. wide (Figs. 1, 3, and 23). The sexes are separate and indistinguishable except for the number of pleopods and the genital apertures. Apparently copulation takes place after invasion of the oyster and perhaps is necessary, as Atkins suggests, in order for further development of the female crab to take place. In *P. pisum* she

<sup>1</sup> The author wishes to express his deep appreciation for the many ways in which Dr. Thurlow C. Nelson aided and inspired this work.

<sup>2</sup> Now situated in the Department of Zoology, Rutgers University.

found that in all other stages of the female crabs the spermathecae contained some spermatozoa. Occasionally only one spermatheca was full but more often both were distended with sperms. Except for a few males similar in external appearance to the second stage females no other stage of the male *P. ostrum* is known and the male is believed to be free-swimming like the invasive first stage female.

The second stage female differs markedly from the first stage being rounder in form, grey in color with prominent chromatophores, with a softer carapace and slenderer legs. In size, however, it measures only slightly larger (0.9–3.1 mm.).

The third stage female is still larger (2.6–4.4 mm. wide) but aside from this is quite like the second stage in color, shape and appearance. Higher development of the pleopods differentiates it from the latter.

The fourth stage female is pale yellow in color and is again larger (3.6–8.9 mm. wide).

The adult female, or fifth stage crab, ranges in size from 6–14.9 mm. and is the form of *P. ostrum* commonly known. Indeed, except for this stage, only a few males and none of the other female stages have ever been recorded. Several moults of the fifth stage female crabs are possible and there is some overlapping of sizes of the crabs in various stages due to time of invasion, food supply, size of the oyster invaded, etc. No data are available on the rate of growth or time lapse involved between the various female stages. Only moults of fifth stage females and one moult of a third stage female into the fourth stage have been obtained in the laboratory. In one dredged oyster a fifth stage female and a moulted shell were obtained within the same bivalve.

Ovigerous females are seen in the summer and autumn of the year and Atkins believes that *P. pisum* may become adult in a single year. There is reason to believe that such is the case with *P. ostrum* also. Judging by the size of the mature female crab, with reference to the male copulatory pleopods, it seems unlikely that a second copulation takes place. Therefore, if the large crabs live more than one year, which is quite probable, they must have received sufficient sperm in the one copulation to last for several batches of eggs or become capable of producing only infertile eggs. Orton and also Atkins found the majority of large females of *P. pisum* to have full spermathecae but an occasional large female with empty spermathecae led the latter to postulate that copulation may occur more than once.

After a time, the length of which is still unknown, the developing embryos hatch from the eggs attached to the pleopods of the mother producing a zooea which has been described for *P. ostrum* by Birge (1882) and again by Hyman (1924). In our own experience an ovigerous female was obtained from an oyster dredged as late as October 19, 1942. The embryos then were almost ready to hatch and showed a pulsating heart, a fully formed abdomen, eyes, a digestive gland, and appendages. Hatching began four days later and large numbers of the first zooea were available for study.

Subsequent planktonic stages of this crab are still unknown but judging by Lebour's (1928) criteria (the relatively primitive condition of the first zooea) three or more zooeal stages are probably present and possibly also a megalopa. Eventually, however, the free-swimming invasive male and female crabs are formed completing the cycle.

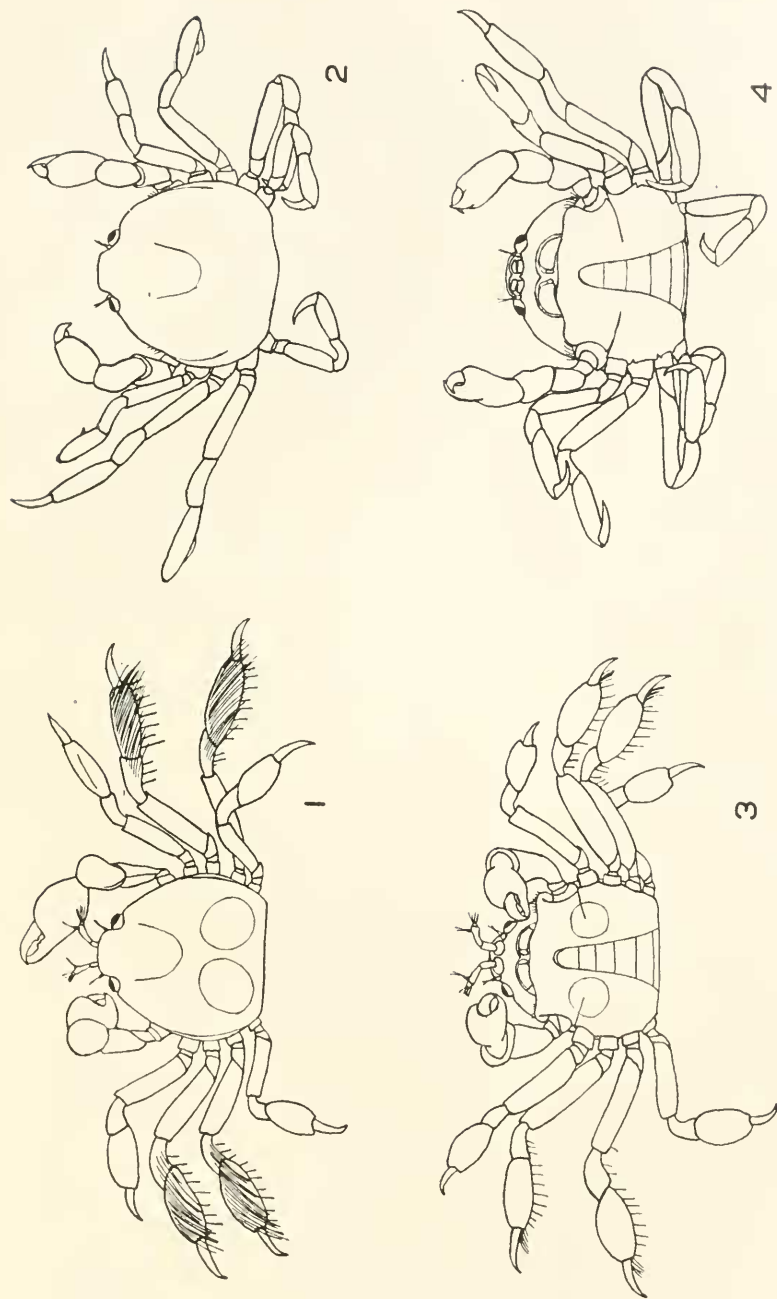


PLATE I

First and second stage female *Pinnotheres ostrum*,  $\times 10$

FIGURE 1. Dorsal view of Stage I female,  $H_{acd}$

FIGURE 2. Dorsal view of Stage II female.

FIGURE 3. Ventral view of Stage I female.

FIGURE 4. Ventral view of Stage II female.

## MORPHOLOGY OF THE VARIOUS STAGES OF THE CRABS

*The male*

In contrast to *P. pisum*, the male *P. ostreum* has been considered an unusual find, Rathbun (1917) reporting only two specimens in the National Museum collection. In size it is much more restricted than the male *P. pisum*, the carapace usually being from 1.5–3.4 mm. wide with sizes below 1.6 and above 2.5 mm. being rarely seen. The mean carapace width of 144 specimens was  $2.13 \pm 0.19$  mm. Furthermore, unlike all but the first stage female from which it is almost undistinguishable, its shell is well fortified with calcium salts probably making it as hard for its size as species of free-living crabs. In color it is dark brown with two large distinct almost circular pale white spots, visible both on carapace and on the sternum. On the posterior half of the dorsal side they are situated in the branchial regions. On the ventral side they flank the groove which contains the abdomen and are situated at the level of and medial to the first pair of pereopods or walking legs. In a male, whose carapace was 2.0 mm. wide the dorsal spots were roughly 0.6 by 0.5 mm. On the ventral side of the same crab the pale areas were only 0.45 mm. in diameter. The carapace is flat dorsally, sub-circular in shape with an advanced, more truncate front than is present in the later females. The posterior margin is straight and the widest part of the carapace about  $\frac{1}{4}$  the distance from the anterior end. The eyes are well developed. The front is about  $\frac{2}{7}$  as wide as the carapace. The lateral margin of the carapace is thin and rather sharply bent from the dorsal side. Antennules are large and antennae small. The epistome is well defined. The buccal cavity is crescentic, arched and very broad from side to side but very short fore and aft. The external maxillipeds completely close the cavity and consist chiefly of the merus fused with the ischium and with the flagellum attached to the inner end. Carpus of the first segment of the palp or outer maxilliped, short, oblong; propodus more elongate, rounded; dactylus inserted behind middle of the propodus, minute and slender. Chelipeds (Fig. 5)<sup>3</sup> are stout, merus and carpus not slender as in the later females. Propodus slightly flattened inside, swollen outside and strongly widened from proximal toward distal end, narrowing again so that width at base of dactyli is considerably less than the greatest width of propodus. Both margins of propodus are convex. Fingers are stout, especially the immovable one with the tips hooked past each other when closed. The movable finger has a small tooth which fits between two protuberances on the immovable finger. Stiff hairs project from the gripping surfaces of both fingers.

The pereopods are markedly flattened with the propodi almost spatulate, the third leg being slightly longer and stouter (Figs. 6–9). The propodi are widest about centrally, being half as wide as long and over twice as wide as thick ( $0.42 \times 0.18$  mm. in one case). The posterior border of the propodi of the walking legs is

<sup>3</sup> Although Figures 5–9, inclusive, were drawn specifically from a first stage female crab, the respective appendages of the same stage male are indistinguishable.

## PLATE II

Ventral view of chelipeds and pereopods of Stage I and II female *Pinnotheres ostreum*.  $\times 54$

FIGURE 5. Cheliped of Stage I female.

FIGURES 6–9. Pereopods of Stage I female.

FIGURE 10. Cheliped of Stage II female.

FIGURES 11–14. Pereopods of Stage II female.



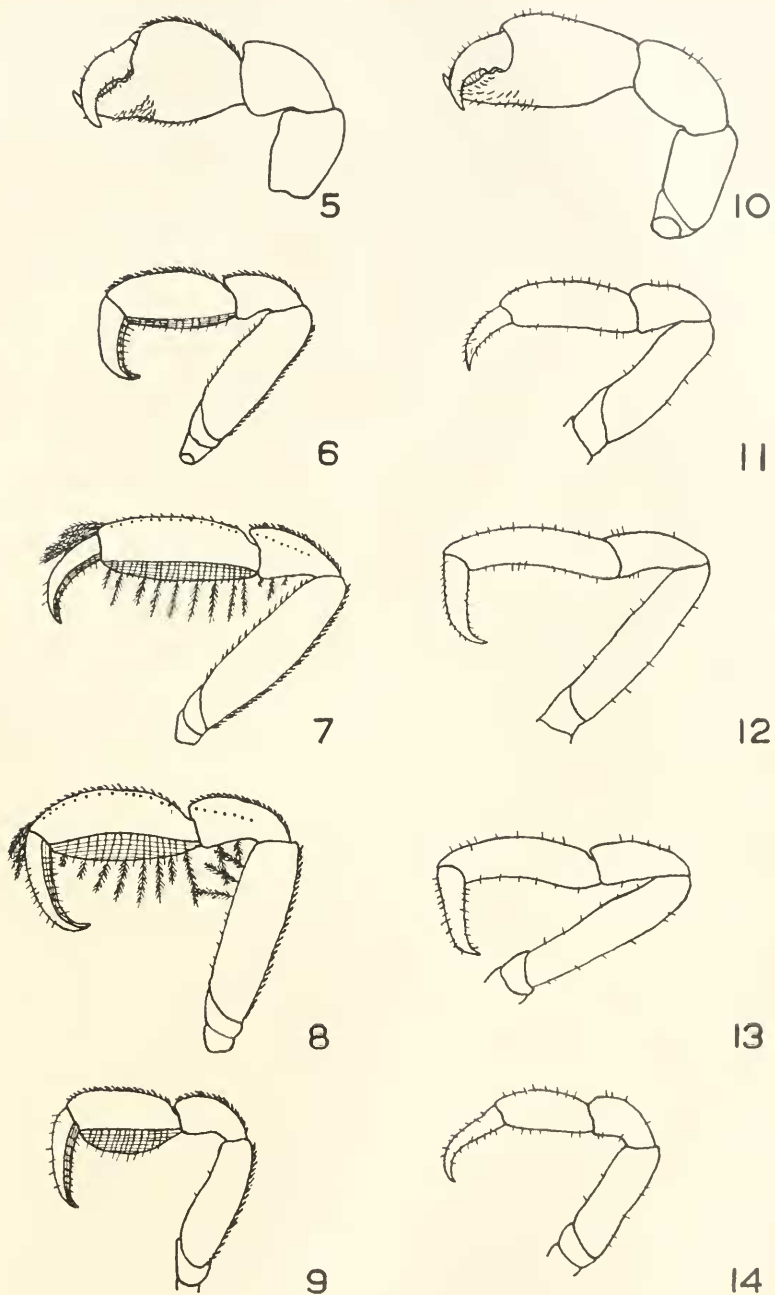


PLATE II

thickened. The amount of thickening is progressively greater from first to fourth walking leg, being not quite half the total width of the propodus of the fourth leg. The thickened portion seems to be constituted of the same material as the rest of the exoskeleton. Not only does it show longitudinal striations as though produced by successive depositions of chitin but the whole thickness is pierced by the hairs which protrude from the posterior border of each of the propodi. The dactyli of the same legs also show a similar thickening of the posterior which is likewise pierced by the protruding hairs. Unlike the female, the dactylus of the third leg of the male is longest but it is not markedly longer than that of the second which is almost as long and a trifle more curved at the tip. Also unlike the adult female, the dactyli of the second and third legs are only slightly more or less than half the length of the propodus of the same leg. There are two rows of long plumose hairs on the second and third legs. One row extends postero-dorsally from the anterior edge of the dorsal surface in a line running from midway on the carpus to the distal end of the propodus. Some of the hairs are over 0.6–0.9 mm. long. The other row extends backward from the posterior border of the flattened leg also extending from middle of the carpus to distal end of the propodus. These hairs are only about half as long as those on the anterior edge. The other joints of these legs and the other legs only possess short hairs or setae which are stout and plumose and are especially abundant on the anterior edges of the propodus, carpus and merus. We consider that these flattened, hairy legs are adaptations for free-living existence. Indeed, the first stage crabs are fair swimmers and reach the oysters by this means. The sides of the abdomen are almost straight and become narrower from the third to the seventh segment (Fig. 16). The terminal segment is arcuate. The abdomen fits neatly into the grooved sternum. A locking apparatus, somewhat like that described by Atkins for *P. pisum*, is present in the male *P. ostreum* (Figs. 15 and 16). It consists of a pair of almost conical chitinous knobs (on the fifth thoracic segment) along the side of the grooved area where the abdomen fits and a pair of larger blade-like protuberances on the sixth segment. Both sets of knobs project slightly anteriorly, ventrally, and medially.

Instead of fitting into grooves on the abdomen there are shelf-like projections on the fifth and sixth abdominal segments. The shelf on the fifth segment is much shallower and smaller than that on the sixth. The knobs on the thorax are hooked under these shelves making a close-fitting efficient locking mechanism that can easily be undone by the crab through extension of the abdomen and lifting but which is

### PLATE III

#### Some details of structure of *Pinnotheres ostreum*

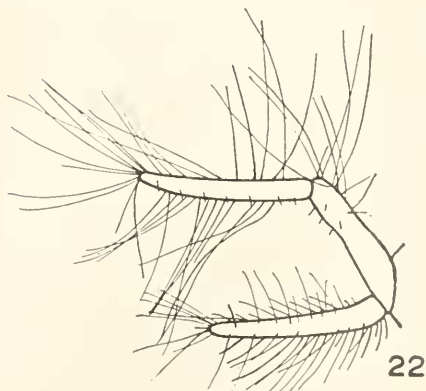
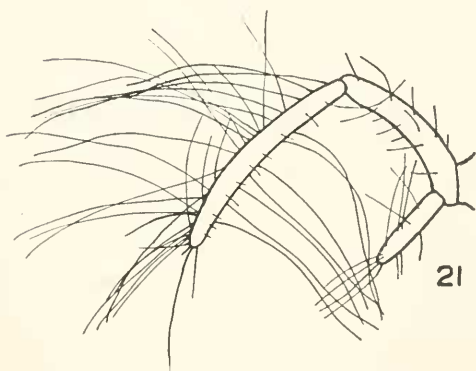
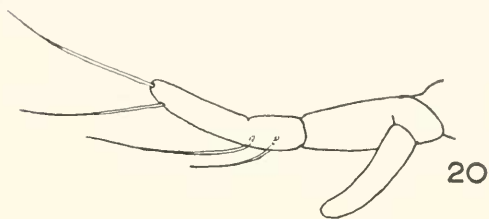
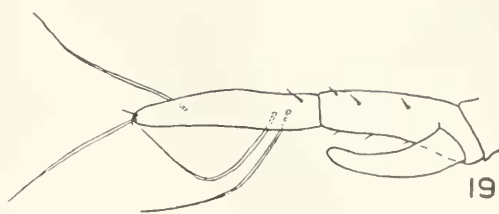
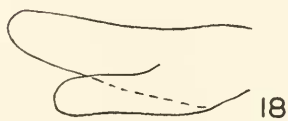
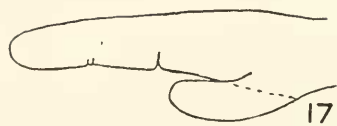
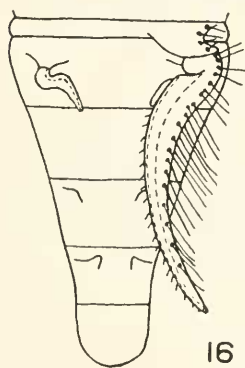
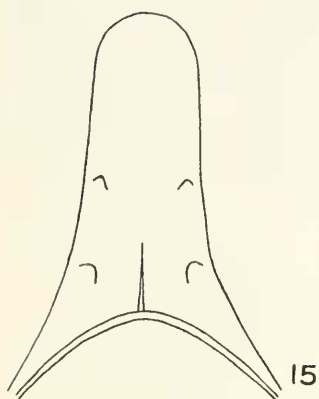
FIGURE 15. Ventral view of the sternum of a male crab (Stage I) showing the chitinous knobs of the locking mechanism.  $\times 20$ .

FIGURE 16. The abdomen of a Stage I male crab showing the copulatory pleopods. The first appendage on the right side was removed to better expose the smaller second appendage. Figure also shows the shelves of the locking mechanism.  $\times 20$ .

FIGURES 17 AND 18. First and second pleopods, respectively, from the left side of a Stage II female crab.  $\times 166$ .

FIGURES 19 AND 20. First and second pleopods, respectively, from the left side of a Stage III female crab.  $\times 43$ .

FIGURES 21 AND 22. First and second pleopods, respectively, from the left side of a Stage IV female crab.  $\times 22$ .



difficult to dislodge in the living animal where the stronger the flexing strain the more tightly the knobs lock.

The only thoracic somite dividing suture on the sternum is seen extending mediad from behind the coxa of the cheliped to a point a little more than midway to the groove where the abdomen lies. This is between the fourth and fifth thoracic segments. The copulatory organs of the male are large, like those in *P. pisum*, the first is blade-like and hairy and the second is rod-like (Fig. 16) and almost hairless. The tube runs along the medial side of the first appendage and the second appendage fits into a groove running across the under surface of the first appendage near the base of the terminal segment. The first appendage is more slender and scimitar-like than the same appendage on *P. pisum*.

### *First stage female*

This is the female stage which invades the oyster (Figs. 1 and 3). It is superficially indistinguishable from the male although it is usually slightly smaller on the average (1.4–2.4 mm.). The mean of 187 measurements of width was  $1.83 \pm 0.14$  mm. Not until careful examination is made of the abdomen and the sternal groove into which it fits can differentiation be made.

For example, there is only one pair of chitinous knobs (corresponding to the anterior pair of the male) and consequently only the terminal or corresponding pair of shelves on the abdomen (on the sixth segment). The genital aperture is small and located just posterior and medial to the base of the chitinous knob on each side. The relationship is thus almost precisely like that in *P. pisum*. The abdomen in the female has slightly straighter sides with the terminal segment having a lower arch. It lacks one pair of locking shelves and the segmentation between 3 and 4 and between 4 and 5 is much less distinct than in the male. Furthermore, the first segment is widest unlike the male where the third segment is widest. Such differences are very minor and usually cannot be determined *in situ* but only by removing the abdomen for comparison. Then, however, these differences are quite constant. Finally, the abdomen of the female bears four pairs of minute appendages, the first one of which is biramous, the second has a bilobed tip, presaging its eventual biramous state, and the other two are simple knobs. The walking legs are like those of the male.

### *Second stage female*

This stage hardly exceeds in size the range of the first stage female. The carapace width of 67 specimens ranged from 0.9 to 3.1 mm. (mean  $2.1 \pm 0.23$  mm.). The moult which occurs involves more differentiation than growth. The carapace is now smooth, shining, thin and membranaceous and, unlike the previous stage, yielding to the touch. It is convex from before backward and the lateral margins are thick and bluntly rounded. The front is still about  $\frac{2}{7}$  the width of the carapace but now it is less truncate and does not project quite so far forward (Figs. 2 and 4).

The chelae are slightly more slender with the propodus widest more distally, nearly at the base of the fingers (Fig. 10). The pereopods (Figs. 11–14) are slender and subcylindrical with delicate hairs on the last three segments. No such plumose hairs are present as described on the Stage I crabs. Propodus is not flattened on pereopods as in Stage I nor does it broaden out very much, being only



## PLATE IV

Photomicrographs of *Pinnotheres ostreum* and gill-eroded oysters. I wish to express my appreciation to Dr. T. C. Nelson for these. He not only took the photographs but found the particular specimens displayed. All  $\times 3$ .

FIGURE 23. View of large-crab type gill erosions in an oyster. Note the presence of both a large Stage V female crab and a small Stage I male crab. The demibranchs of the oyster are shorter than normal and the ventral mantle cavity much enlarged.

FIGURE 24. Small-crab type erosions of gills. Note the sharply-delimited, punched-out area involving three demibranchs.

slightly wider than the merus of the same leg. The third leg again is largest and the dactyli of second and third legs nearly equal in length.

The abdomen is approximately the same shape as in the first stage. The ratio of carapace width to abdomen width is 2.46 and of abdomen length to abdomen width is 1.36. The first is still the widest segment. The terminal segment is only slightly wider ( $1\frac{1}{2}$  times) than long in this stage. The sternum is still deeply grooved to hold the abdomen flush. Chitinous knobs are still to be seen on the thorax but the mechanism is now weakened by the delicate nature of exoskeleton.



This is obvious the first time one attempts to lift the abdomen. In Stage I males and females this is accomplished with difficulty and often the abdomen is injured in the process. In this and subsequent stages lifting of the abdomen is easy. Here is an adaptation to the sheltered life within the mantle cavity of the oyster which free-living first stages do not show. The legs also, no longer needed for swimming, have become slender and relatively smaller with each stage of development.

The abdominal appendages are but little advanced over those seen in the first stage female though in some instances they seem farther along than others. This and subsequent stages, while rather clearly defined, do vary quite broadly within the stage. In some there seems to be little change over the appendages of the first stage female, in others the biramous character of the first two pairs is more clearly marked. The appendages are still hairless, small and relatively undifferentiated (Figs. 17 and 18). There are many chromatophores scattered over carapace, sternum and abdomen. The legs have few of these black chromatophores although the chelae are well supplied. Consequently, the crab in this stage, against a light background, appears mottled grey with translucent appendages. Against a dark background, the appendages show up better and appear opaque. The later stages, especially the third stage female, are quite similar in color but cream-colored specimens are seen in increasing abundance. This is due chiefly to the decrease in numbers of these chromatophores and dispersion of pigment within them, and an increasing opacity of the organs within the crab. The adult female is always cream-colored except for the reddish outline of the mature gonad, the anterior parts of which are seen through the carapace from above and the posterior parts through the abdomen from below.

#### *Third stage female*

The chief differences are those of size, shape, and relative size of abdomen and character of the abdominal appendages. The width is from 2.6–4.4 mm. (mean of 31 specimens was  $3.17 \pm 0.40$  mm.). It was found less frequently than first or second stage crabs in 1941 but has been relatively more abundant in 1942. The second and third walking legs are nearly equal in length with the dactyli also almost the same length. The average ratio of carapace width to abdomen width in eleven specimens was 2.0 and that of abdomen length to abdomen width was approximately 1.1. Thus the width of the abdomen has relatively increased slightly over both the length of the abdomen and the width of the carapace. In most of the specimens the third or fourth segment was widest. The terminal segment of the abdomen now has a flatter arch, usually being over twice as wide as long. The abdominal appendages, especially the first two pairs, are clearly segmented and possess a few distinctly plumose hairs (Figs. 19 and 20). The edges of the abdomen now extend beyond the broadened and shallower depression in the sternum which in earlier stages wholly contained the abdomen. There are hairs on the lateral edge of the abdomen in this stage. These hairs are more abundant on the more proximal segments and are quite variable in number. They are stout, plumose and rarely exceed 0.15 mm. in length.

#### *Fourth stage female*

Specimens on hand range in size from 3.6–8.9 mm. The abdomen is much broader now and just reaches the coxa of the legs in the majority of specimens.

It extends forward almost to the posterior edge of the mouth. The sternal depression is much broader in this stage though the abdomen overlaps it considerably. The third or fourth abdominal segment is widest and the abdomen wider than long even when pressed out flat. The carapace-abdomen width ratio has also further decreased and is now nearly equal to 1.0. The terminal abdominal segment has broadened to such an extent that it is now three to five times as wide as it is long. The abdominal legs are almost fully developed and well supplied with hairs (Figs. 21 and 22). The hairs along the lateral edge of the abdomen are more numerous and large and are present on all segments as a uniform fringe in the fourth stage crab.

The orbit has hardly increased in size and the diameter of the eye is practically the same. Thus the relative prominence of the eyes has decreased markedly. The carapace is now much more convex so that the front appears to be ventral in position. The abdomen is very convex externally and cannot be flattened without tearing the exoskeleton. Ventrally the hollowed abdomen is suited for carrying the masses of ova.

#### *Fifth stage female*

This is the stage commonly seen. The prominence of the reddish gonads identifies it in most cases though some fifth stage females are found with immature gonads. A few apparently fourth stage crabs show mature gonads, however. The features which differentiate the fourth and fifth stage females are rather slight. The abdomen is now wider than the carapace, extending to the basis of the walking legs in many cases. The terminal segment is more than five times as wide as long. The abdomen projects forward to a point anterior to the mouth which it covers except when feeding. For this act it rolls inward the terminal segments exposing the mouth parts as described for *P. pisum* by Orton. The size ranges from 6.0–14.9 mm. (34 specimens measured). It is possible that adult size is determined in part, as Atkins found for *P. pisum*, by the size of the host invaded. Even here, however, the range is great. Thus, a fifth stage crab 9.0 mm. wide was found in an oyster only 29 mm. long. Its abdomen was 12 mm. wide and extended beyond the coxopodites. No studies relating host size with crab size have been made but such a factor would account partly for the overlapping sizes of the various stages of the female crab. Another factor would be subsequent moulting after the fifth stage is reached. This is known to happen and several fifth stage females have moulted in the laboratory. Since only one moult of an earlier stage has been obtained which resulted in the production of a fourth stage female from a third stage crab, it is not known whether all earlier moults involve metamorphosis or whether growth moults can occur between stages. Biological variability and amount of available food are probably additional factors in size variations.

The walking legs of the adult female are different in their proportions from the earlier stages for the second leg is distinctly longer than the others and the dactylus of the second leg is more than two-thirds as long as the propodus. In our specimens, however, it does not seem to be regularly seven-eighths as long as Rathbun described it.

Two ovigerous females are present in our collection, the first measures 14.0 mm. across the carapace but the other only 8.9 mm. This is a further indication of the variability existing in the stages of the crab.

*Second stage male*

The presence of a number of specimens similar in external appearance to second or third stage females (body shape, exoskeleton yielding to the touch, slender, translucent legs, and grey or cream in color) has been noted. Thirteen measured specimens averaged 3.1 mm., ranging from 2.0–4.8 mm. Shape of abdomen and presence of typical male pleopods clearly identify these crabs as males. The pliable abdomen, however, only has one pair of the shelves of the locking mechanism though the sternum still shows both pairs of chitinous knobs. Like the females (except those of Stage I) the exoskeleton is delicate in these soft-bodied males and the abdomen can be easily lifted from the sternum even in living crabs. Since these crabs have been found in appreciable numbers it is quite possible that they may serve as partners in copulation with larger females of later stages though no evidence is available for or against this possibility. The size range would indicate that at least one, and probably two, moults can occur beyond the typical hard-shelled first stage males. It is also possible that these atypical males are the result of some sort of parasitism as Mercier and Poisson (1929) have reported for *P. pisum*. They found that males parasitized by the entoniscid, *Pinnotherion vermiforme*, resembled immature females in increased size and decreased firmness of the carapace and in the diminished number of hairs and greater slenderness of the legs. Parasitized female *P. pisum* were not perceptibly modified in these characteristics.

## PRESENCE OF PINNOTHERES IN OYSTERS

All the stages of the crab described in the preceding pages were found in oysters from Delaware Bay in both 1941 and 1942. Although multiple infestations occurred involving various combinations of the crab stages, no case has been found containing more than a single specimen of either the third, fourth, or fifth stage crabs. First stage males and females were in great abundance in 1941 but were much less frequently seen in 1942 either per oyster opened or proportionate to the other crab stages. This is indicated in Table I where the same grounds of oysters were sampled in the two years. The only differences were that the oysters in each case were a year older in 1942 and that a twenty-five to thirty-three per cent mortality had occurred on each ground during the intervening winter.

TABLE I

*Distribution of numbers and stages of P. ostreum in oysters from two grounds sampled in consecutive years*

Ground	Year	Mean no. of crabs per oyster*	Max. no. of crabs per oyster	Oysters with crabs	Stage I crabs	Stage V crabs
A	1941	6.0	18	80%	91.4%	1.2%
	1942	1.1	3	73%	41.7%	33.3%
B	1941	4.2	19	80%	92.0%	1.6%
	1942	1.1	5	55%	50.0%	30.0%

\* Based on total number of oysters in the sample.

We offer the data in this table also as additional evidence in favor of Atkins' belief (although she was working with *P. pisum*) that growth to maturity takes place within a year's time. The marked increase in both absolute and relative numbers of Stage V crabs in relation to a marked decrease in total crab population is more than suggestive.

The greatest number of crabs in a single live oyster was seen in 1941 when 262 crabs were found in an oyster measuring  $85 \times 46$  mm. This oyster was in a sample dredged from Ground C already showing a high oyster mortality. Of the other live oysters in this sample, 54.6 per cent had more than 10 crabs present within the valves. Other high counts were 32, 63, 65, 81, 112, 134, 154, and 165 crabs per oyster. Multiple infestations have occurred even in small oysters, one dredged from Ground C, measuring only  $32.4 \times 14.7$  mm., containing eighteen first stage crabs.

Besides oysters containing only a single specimen of any crab stage, almost all conceivable combinations of crabs have been found among the multiply-infested oysters except those involving the larger stages.

The only other cases of multiple infestations with crabs of the genus *Pinnotheres* were reported by Ohshima (1927). As many as seven male *P. latissimus* were found within the shells of a single specimen of *Paphia*.

The crabs when present in small numbers are usually found in the mantle cavity but in the heavier infestations crabs are found throughout the water conduction system of the oyster. An extreme case is that of the multiply-infested oyster dredged in September, 1942. The mature fifth stage female crab and five first stage crabs were found on the oyster's gills, three other first stage crabs were found in the cloacal chamber and one each in the promyal and the right and left supra-branchial chambers. In one interesting case the oyster when opened disclosed a Stage V female on the gills and a Stage II female in the promyal chamber. In another case three Stage I females were found one each in the promyal and left supra-branchial chambers and one at the exit of the promyal chamber.

When only a single crab is present it is usually found on the gills (in the mantle cavity) and females of Stages III, IV, and V have been found only in this area. We may state, therefore, that this is the normal position and that aberrant positions increase with the number of the invading crabs.

Orton (1921) reported a similar state of affairs with reference to *P. pisum* in *Mytilus edulis*. Observing the feeding of these crabs through windows in the mussel's shell he noted that the larger crabs sit on the middle of the mussel with a pair of gills on each side. The smaller crabs, he reported, may be found anywhere in the mussel but generally on the gill.

In Delaware Bay, oyster crabs are found in oysters from every area sampled to date. Since this included oysters well up the bay in regions of relatively less saline waters we may state that *Pinnotheres ostreum* is able to survive wherever the oyster can. Such a statement needs some qualification, however. Invasion of oysters by a new brood of young crabs probably occurs in late summer and autumn when the haligraphic picture of the bay waters (based on extreme data for more than seven years) is almost always at or above the mean annual level of salinities in the bay (Stauber, 1943). The meager data at hand indicate that if markedly low salinities prevailed at this critical time survival of the crabs would probably be greatly lessened. Crab-infested oysters subjected to adverse environmental conditions throw



considerable light on this problem. Death of first stage crabs within the oyster has occurred as a result of over-winter storage of oysters in pits in the ground and in a home refrigerator and as a result of the subjection of oysters to periods of low salinities (spring of 1941 and late autumn of 1942 on the beds far up the bay). It is especially notable that the later stages of the female crabs were able to survive these same adverse conditions. The latter fact is clear evidence that the adaptation of the crab to life within the oyster, as is indicated by the morphological changes of the female crab, involves physiological changes as well. Since the adverse situations described above all involve persistent closure of the oyster the female crab acquires the ability (which the oyster is well known to possess) to survive periods when cessation of the food supply and interruption of a steady stream of oxygenated water for respiration occur.

Invasions of oysters by *Pinnotheres* most probably occur in the late summer and autumn. This statement is based on several types of observation. The few ovigerous females seen have been encountered only during this period. Besides, crab zoeae of various species are found during these seasons. Furthermore, the 1941 mortalities began to be noticed in September of that year. Finally, infestation of oyster spat only a few months old was observed several times. Such invasion could only have occurred in the late summer or early autumn.

The heavy crab infestations of oysters reported in Table I were extreme values. In most areas sampled fewer than twenty-five per cent of the oysters opened contained crabs of any size, Stage V females being in the great majority. In such samples multiple infestations were very unusual. This is as valid for 1941 when the general incidence was much higher as it is for 1942.

Oysters of all sizes have been found infested with crabs. All stages of crabs have been found present though no later stages of females have been seen in oysters less than one year old for reasons which are obvious. The smallest infested oyster was one less than four months old from the egg and only  $20 \times 16$  mm. in size. A second stage female crab measuring only 0.9 mm. wide was found in the mantle cavity. The left mantle was perforated and the inner right demibranch slightly eroded. These observations indicate that growth and differentiation of the crab and perceptible damage to the oyster can occur within a relatively short period of time.

The smallest oyster yet opened which has contained a mature fifth stage female was an oyster probably less than two years old and measuring only 34 mm. long. The crab had a carapace 9 mm. wide and large-crab type gill erosions were present.

#### MODE OF FEEDING

Orton's description of the feeding of *P. pisum* in *Mytilus edulis* is remarkably similar to the method of feeding of *P. ostreum* in the oyster. The larger crabs are stationed with ventral side approximated toward the inner aspect of one mantle and facing away from the oyster's gills toward the ventral margin of the shell or into the incurrent stream of water. Usually two of the oyster demibranchs project over and above the carapace of the crab and not in regular contact with the crab. The other two demibranchs are close to and at times in contact with the posterior part of the ventral surface of the crab.

The oyster feeds by straining sediment and plankton (chiefly diatoms and dino-



flagellates) from the water.<sup>4</sup> A portion of these strained particles mixed with mucus is passed anteriorly in trails along the marginal furrow of each demibranch. The palps of the oyster constitute a further sorting apparatus and some of the strained material is rejected by the palps. This rejected material is passed posteriorly and ventrally along a ciliated path on the inner aspect of the mantle to a point near the ventral edge of the shell from which it is ejected by the blowing force of the sudden closure of the oyster's valves. If the oyster crab confined its feeding activity to the constant stream of rejected material on its way from the palps it might be of some value to the oyster and could possibly be called a symbiont or at least a commensal. However, in our experience the rejected masses are too bulky to easily fit into the crab mouth and most of this material is eventually thrown off by the crab after attempting to break it up into suitable particles by the action of the mouth parts. By reaching beneath its abdomen with its claws and also by disengaging the tangled mucus-food masses caught in its legs, it obtains newly-formed, delicate, strings of food much more capable of being handled by the mouth parts and ingested. I have seen such strings completely and quickly engulfed. The crab often combs the other legs with the chelipeds to free them from entangled food masses. The mucous masses are then passed to the mouth where the mouth parts in turn gather and press the strings of food into the mouth. The fourth or last pair of walking legs are frequently worked up over the carapace of the crab to scrape forward within the easy reach of the chelipeds any food strings which may fall from the other demibranchs or even to disengage them from the marginal furrow. The large crabs range in the mantle cavity from the place where palps and gills meet to a point ventral to the adductor muscle. Under favorable conditions they are seen to be very active, almost constantly moving legs or chelipeds.

The process of feeding, however, is wasteful and much of the material brought to the mouth is handled several times before it is ingested with appreciable amounts thrown off by the mouth parts. In one case a large crab was straddling the stream of rejected mucus-food passing to the edge of the mantle from the palps yet in more than fifteen minutes' steady observation it failed even to attempt to pick it up. In the meantime the combings of the walking legs were being vigorously prosecuted.

Rathbun remarks that the food of the oyster crab is composed of the same organisms which constitute the food of the oyster plus small crustaceans not normally the food of the oyster. The complicated feeding mechanism of the oyster is chiefly one of straining particles from the water and then sorting out and discarding the larger of these particles. Much of the food passing along the marginal furrow is destined to be discarded because of particle size. It is not surprising, then, that small crustaceans (Rathbun) are included in the crab's diet in addition to the entangled smaller organisms eaten by the oyster.

Observations on the feeding of the smaller stages of *P. ostreum* (especially first and second stages) throw further light on the mechanism producing the gill damage to be described later. In maintaining its position on the demibranchs the pointed dactyli of the walking legs are regularly seen to pierce the gill tissue. In order to maintain its position several nearby plicae may be stretched out of position by the pull of the inserted dactylus. When the leg is moved the area pierced stands out as

<sup>4</sup> This description is based chiefly on the findings of Yonge (1926), Elsey (1935) and especially Nelson (1938 and personal communications).

an opaque spot on the demibranch. It appears like a condensation of tissue either by compression of surrounding parts or by invasion of leucocytes. This area is visible to the unaided eye for several hours. Some of the walking legs have been observed to scrape the gill in an attempt to engage mucous strings of food moving on the filaments (especially the principal filaments in the folds between the plicae). This scraping action may be very vigorous and may be likened to the child's use of its fingers to clean the frosting from the egg beater. Occasionally the dactylus of the scraping leg catches in a portion of the gill (ostium). The crab strains and the gill tissue stretches. When the pull becomes hard enough the leg finally completes its motion (due to the local tearing of the gill) and the affected portion of the demibranch springs back into position. The leg and cheliped would then be approximated and the combing would proceed even when no food material had been obtained by the active leg. (Since many of these observations were made in very clear water there was little material to be filtered by the oyster.) Small crabs have also actually been seen to grasp the delicate gill tissue with the cheliped and put tension on it, pulling it out of normal alignment. When released the gill was seen to be definitely injured.

In all stages of the crabs the activity was seen not to consist so much of movement from place to place but chiefly movements of legs and chelipeds related to the act of feeding.

#### INJURY TO THE OYSTER GILL AND GILL REGENERATION

Although no extensive erosions of gills were produced by crabs in the laboratory, nevertheless, the observations recorded and the activities and injuries discussed above are sufficient to account for the extensive gill damage regularly seen in crab-infested oysters.

Two general types of gill damage were noted associated with large and small crabs respectively. The large-crab type erosion (Fig. 23) shows extensive shortening in the height of one or more demibranchs over an area reaching from the anterior end of the gills where they meet the palps to a point usually ventral to the adductor muscle. The affected demibranchs may be even less than half as high as would be expected normally or as the unaffected demibranchs of the same oyster. The outer demibranchs are normally shorter than the inner ones but cases where both inners and one outer are eroded have been seen. Such specimens show the uneroded outer demibranch to be the highest but only in the region where the other gills are eroded. The edges of the eroded demibranchs are usually slightly ragged, markedly thickened, and considerably more opaque than the edges of normal oyster gills. As a result of the gill erosions as well as the more rapid growth of the mantle and shell in a ventral direction along with the growth of the crab, an enlarged mantle cavity is produced permitting ample room for the movement of the contained crab. One oyster examined demonstrated the extreme condition which could develop as a result of the presence and activity of a large crab. The oyster was 7.0 cm. long from hinge to bill and 4.8 cm. wide just anterior to the adductor muscle. The periphery of the mantle extended to the edge of the shell in all directions. The distal margin of the demibranchs, however, did not reach the ventral shell margin by 2.1 cm. at the widest part of the oyster. The left demibranchs were only 0.8 cm. high and the eroded right demibranchs only half this size. The fifth

stage female crab was 13.0 mm. wide but with outstretched legs and chelae she extended over an area 4 by 2 cm. At first glance after turning back the mantle the body of the oyster appeared to occupy only the dorsal half of the cavity formed by the two shells.

The position of the crab within the oyster was studied in relation to the orientation of the oyster on the bottom. It was found that the crab always faced away from the gill with the normal gills over the crab's carapace (Fig. 23) even when the oyster's position on the bottom made it certain that the crab had remained consistently upside down with relation to the earth's gravitational field. In the laboratory also, there were numerous cases where the crabs remained for days in an upside down position on the oyster's gills. It is this persistent maintenance of position associated with the feeding activities of the crabs which produces the type of erosions seen.

The small-crab type erosion is quite different in appearance and consists of a more local, sharply delimited erosion of one or more demibranchs (Fig. 24). Any single or contiguous demibranchs may be eroded or even all four. The earliest cases show a ragged distal edge, but further attack gradually hollows out a space in which the crab is found. The picture reminds one of a portion cut away or punched out of the edge of the gill although in two cases one of the eroded demibranchs was perforated. The margins of the damaged area are usually thickened by what appears to be accumulations of leucocytes and probably regeneration of damaged tissue. Small-crab type erosions are usually seen at the anterior ends of the demibranchs though, occasionally, typical erosions are observed at any point along the gill. The demibranchs are often eroded more than half way to the base. Very rarely in multiple infestations two areas of damaged gill are seen. Except for one case of eroded palps and several cases with a perforated or damaged mantle area in close approximation to typically eroded gills no other sites of injury to the oyster have been found. In a few cases the mantle instead of being actually perforated was blown up into a "blood blister" or a "pus pocket" as a result of the irritating activity of the crab. The localization of injury is almost conclusive proof that gill destruction is produced by the impingement of the crab's method of feeding on the oyster's food-sorting equipment. It is most likely that the initial break in the marginal furrow by causing food trails to end at the break results in intensified activity by the crab at this spot. Such gill damage is not necessary to but incidental to the mode of feeding of *Pinnotheres*. In the case of the first stage crabs, however, the exoskeleton is hard and unyielding. Certainly this contributes to the production of the early lesions though extension to the large-crab type must occur in later stages of development. Since the adaptation of the crab to the oyster has not yet reached a plane where neither suffers injury the oyster-crab, *Pinnotheres ostreum*, must be considered parasitic on the oyster. It is conceivable that further evolution by shortening the feeding time of the first stage crabs, further decreasing the strength of the exoskeleton, increasing the skill with which the crab obtains the mucus-food strings or confining its feeding to the palp-rejected masses, might result in a relationship less harmful to the oyster. The crab would then be a more efficient parasite in Swellengrebel's (1940) sense of the word.

In small-crab type erosions the gill damage frequently extends down to the base of the gill such that the suprabranchial chamber is directly visible through the most proximal portions of the water tubes. Previous types of damage described involve

chiefly a decrease in total gill surface available for feeding. The exposure of the water tubes illustrates another type of malfunction of the oyster's feeding mechanism which has been studied in more detail in the laboratory.

When the oyster's gills are experimentally damaged it can be shown that such injuries produce leaks in the water conduction system of the oyster. Since such a leak backward into the mantle cavity means that water already strained must be rehandled several times a decrease in gill efficiency results the degree of which depends on the extent of the leakage. In a typical experiment a dissecting needle was pushed into the inner left demibranch of a small oyster (No. 1) on the half shell (opened six days before) and forced distad tearing a single plica for a distance of approximately 1.8 mm. from the marginal furrow. When the surrounding plicae were tested with ink suspension<sup>5</sup> some of the latter was seen to escape from the torn plica. A portion of the water being strained by six adjacent plicae was observed to be leaking back into the mantle cavity.

When more extensive V-shaped areas were cut out of a demibranch by scissors the leakage was much greater in volume and water strained from a much larger area was involved. A market-size oyster (No. 2) opened and studied on the half shell will serve as a typical example. Such preparations live as long as six weeks in aquaria, especially if water temperatures are generally below 20° C. A wedge of the outer left demibranch was cut out which measured about 1 cm. across the widest part (along the marginal furrow). At the apex the cut penetrated to a point slightly more than halfway to the gill axis or base. The excision was located just posterior to the anterior third of the demibranch. When ink suspension was placed on this demibranch anterior to the cut practically none escaped in the normal fashion from the cloacal chamber but streamed forcefully out of the openings of the severed water tubes. In consequence, the water strained by more than a third of one demibranch had to be rehandled. Ink placed on the inner left demibranch at the level of the cut on the outer left demibranch also escaped in large part from the cut water tubes of the outer left demibranch. Such a loss of efficiency of parts of two gill leaves must reduce the amount of food an oyster can obtain.

As a result of these findings newly-opened, crab-infested, gill-eroded oysters were studied to see whether such leakages occurred naturally. For reasons to be discussed later; namely, the rapid rate of healing and regeneration of the oyster, good examples were hard to find. One notable case, however, examined in January, clearly demonstrated the existence of such injuries. Water tubes of the two inner demibranchs were exposed in the central portion of a rather extensive small-crab type erosion. When tested on the half shell with ink, both affected demibranchs showed significant leaks. Not only the usual loss from ink placed anteriorly to the lesion but even some placed posteriorly escaped from the damaged area. The latter indicates that some water was moving *anteriorly* in the supra-branchial chamber above the inner right demibranch for a short distance.

<sup>5</sup> The ink suspension is made by diluting Higgins' Eternal Black Carbon ink with bay water. A dilution of about 1-10 with some subsequent evaporation makes a suspension suitable for use. Placed on the gill of a normal oyster the particle sizes are generally so small that almost all the ink is swept through the ostia into the water tubes. In the intact oyster it appears as a cone-shaped black cloud issuing from either or both of the exhalant chambers on the dorsal side of the oyster.



In another experiment a small oyster on the half shell was placed in a dish with four second stage female crabs. Three days later parts of the demibranchs showed twisted and fused plicae (healed), broken plicae and irregularities of form of filaments not normally seen. One particular area showed extensive damage of nine plicae including destruction of the marginal furrow of eight of these.

To explain the fact that serious leaks are not often naturally found we studied the daily changes in experimentally produced gill lesions of oysters on the half shell. The lesions healed in such a remarkably short period of time that we can easily understand our previous difficulties.

In oyster No. 1, for example, twenty-four hours after the gill injury was produced marked healing had occurred. Three days later (water temperatures in intervening period below 10° C.) much of the damage had been repaired. Anatomically, as well as by ink test, the hole had been plugged by tissue though reorganization of filaments and the marginal furrow had not occurred.

Another small oyster (No. 3) healed much more rapidly. In this case ink escaped from three small experimentally injured areas when tested soon after injury. Less than 24 hours later the holes were sufficiently bridged over by local contractions and regeneration to make water tight plugs.

Another small oyster receiving wedge-shaped excisions of both left demibranchs healed over the exposed water tubes of the shallower one and more than half of the more seriously damaged one in less than a day. Total closure of the wound was accomplished by the fourth day.

Oyster No. 2 likewise healed over though here the excision was so broad and deep that a longer period was necessary for recovery. At the twenty-four interval little microscopically-visible healing could be seen but loss of ink occurred only when placed over a space extending twelve plicae anterior to the excised area. A large amount of ink placed on the inner left demibranch at the level of the injury still showed some loss from the exposed water tubes of the outer left gill leaf.

By the fourth day almost half the exposed openings were bridged over with tissue. On the sixth day ink placed more than two plicae anterior to the edge of the excision no longer escaped from the cut water tubes. When placed proximal to the cut, ink escaped from less than half the originally exposed water tubes and then only at the apex of the wedge where the most exposure occurred. Now, also, only a small amount of the ink placed on the other demibranch (inner left) was lost at the cut surface. By the tenth day microscopic examination and ink tests showed that the gap had been completely closed. Although the damage was not yet all repaired the most serious effects were circumvented. It is reasonable to suspect that the intact oyster under more favorable conditions could respond even more quickly than has been demonstrated in these experiments. Since the crab probably does not confine its activity to a single plica for any considerable length of time a reasonable explanation of the appearance of the gill erosions in recently-opened oysters is at hand.

Gill-damaged oysters lose their crabs at times or eject dead ones. Eventual reconstitution of essential gill structure may then take place though cicatrization and "scar" formation are noticeable. None of the interesting histological aspects of the healing process have yet been studied.



## OTHER EFFECTS OF INVASION

Oysters exposed to prolonged storage in air or earth were found to vary in their keeping qualities. It was soon noted that most of the weaker oysters were crab-infested. Whether this was due to the poorer condition of the oyster, irritation by the crab or greater loss of shell liquor due to the enlarged mantle cavity is not known. From the commercial viewpoint, however, this is a serious matter. Much of these losses automatically are circumvented because the oysterman selects for market only his best oysters. It should be emphasized here that even in multiple infestations the presence of more than one gill erosion is extremely rare. An oyster containing fifty crabs is more likely to have no greater eroded area than an oyster containing only a single crab. It is our belief, therefore, that multiple infestations are the result not only of the presence of large numbers of invasive crabs in the water but also of the weakness produced by the activity of a primary crab invasion or any other condition producing weak oysters. The malfunction or even complete stoppage of the feeding mechanism under such conditions may account for the lack of further gill erosions. Such oysters were probably unable to survive the winter and contributed to the heavy mortalities which occurred in some areas after the winter of 1941-1942.

## INVASION OF OYSTERS BY CRABS

Orton believes that the hard, flat shell of the invasive first stage crab (*P. pisum*) is of value not only in slipping within the valves of the mollusc but in avoiding crushing by the closing valves. We believe this to be largely true for *P. ostreum* and the oyster, though successful invasion does not always occur.

In one experiment an oyster dredged for market was placed in an aquarium with one hundred and fifty first stage *Pinnotheres*. The crabs were scattered over the dish at the start of the trial. Within a short time many were seen lined up around the oyster from hinge to bill mostly at the places where the two valves come together. Seven days after the start only twenty-five live and twenty dead crabs were found in the dish but none were now present on the oyster. The oyster was then opened. There were forty-nine live crabs in the left valve on opening, most of these were around the edges of the shell on the incumbent side where the oyster had apparently begun to wall off the crabs. Twenty-six more crabs were found on the ventral side of the oyster, mostly on the gills but no gill erosions were present. Sixteen crabs were on the dorsal side, three in the promyal chamber, two deep in the cloacal chamber, three deep in the left suprabranchial, three in the right suprabranchial chamber and two so deep in the water tubes of the anterior end of the inner right demibranch that the gill had to be dissected to free them. The oyster was 108 × 66 mm. in size and contained one hundred and four of the crabs. All but one of the original crabs were found. Two of the other trials with various oysters yielded invasions of seventy-seven of one hundred and eighty-one and forty-nine of one hundred and twenty-nine crabs.

In all trials a few dead crabs were seen and in one series of closely examined oysters exposed to only a few crabs the fate of several was followed. A typical case showed a crab attached to the oyster shell opposite the opening of the cloacal chamber. It had assumed this position within a half hour and almost appeared as

though its posterior end were caught within the oyster's shell. Seven hours later it had scarcely moved in position but one hour later it was found on the bottom of the dish on its back, dead, directly below the position it had been occupying on the shell of the oyster. It had apparently attempted entry and partially succeeded but was compressed until dead and then ejected. In another case a weak crab was removed from the bottom of a dish for examination. It had lost parts of two legs on one side. In still another instance two specimens which had effected entry, so far as could be detected, were later ejected from the oyster as dead crabs. These probably had effected almost but not complete entry.

#### NOTE ON COLLECTING SPECIMENS FOR FUTURE STUDY

In commercial packing of oysters the oysters are drained—in part to insure accurate measurement of the volume of the oysters opened. This volume is the basis of paying the shucker or opener. The oysters are later washed and drained again before shipment. Catching the first drainings in pails and then placing the material collected in shallow pans or dishes of bay water allows the crabs, freed in the opening of the oysters, to be readily recognized and collected.<sup>6</sup> We have been successful in obtaining specimens of all stages of *P. ostreum* in this fashion especially from areas where crab density is very low.

#### DISCUSSION

It is obvious from the data presented that *Pinnotheres ostreum* can no longer be considered other than a parasite of the oyster. That we witnessed a most unusual sequence of events in 1941 is without question for the dramatic appearance of an oyster containing one hundred or more crabs can hardly be overstated. The subsequent decrease of numbers in 1942 is another example of the population cycles so often seen in nature. We have also seen the abrupt rise and fall in numbers of starfish, *Stylochus ellipticus* and *Polydora ligni* (Nelson and Stauber, 1940), on the oyster grounds in Delaware Bay in recent years. The rise of each was associated with heavy, localized mortalities.

It is not surprising that the evidence gathered here was not previously noted. The small size of the first stage crabs and the need for careful opening and search of oysters in order to detect their presence are prime reasons. For example, we have repeatedly seen cases with gill erosions but could detect no crab on the first examination. Placing these oysters on the half shell in dishes of bay water for a few hours a subsequent examination would often reveal the presence of a crab. Furthermore, among oysters held out of water for a time we have found specimens of first stage *P. ostreum* dried fast to the edge of the oyster's shell as though they had attempted to leave the unfavorable environment and were trapped by lack of an ambient fluid medium in which to move. This being the case it would take such an unprecedented increase in density as occurred in 1941 to focus one's attention on the causal relationship between crab and oyster gill damage. The very fact that in over one hundred years only two specimens of male crabs were obtained by collectors is in itself suggestive. Nor can the fact that oystermen always select for quality of meats be overlooked. Only someone searching for and among poor oysters or investigating causes of mortality would be apt to find the crabs.

<sup>6</sup> I am indebted to Dr. T. C. Nelson for this fruitful suggestion.

The large crabs, however, have long been known and their very existence means that the earlier stages were also present though undetected. Dean's description of malformed or stunted palps with thickened outgrowths is clearly indicative that the parasitism has not been acquired recently. But the shortening of demibranchs on the affected side of an oyster containing a Stage V crab is not always readily distinguished especially since there are minor differences in the heights of the demibranchs normally. In a significant proportion of the cases also, since the erosions are present on only one or two of the demibranchs, the damaged area is shielded from cursory glance by the unaffected gills which cover them. This is even true of the small-crab type lesion in many cases.

It would be of great interest to learn whether these findings are duplicated at other points along the eastern seaboard where the presence of *Pinnotheres ostreum* within the valves of *Gryphaca virginica* has long been known to exist.

### SUMMARY

1. All the parasitic stages of *Pinnotheres ostreum* are described, many for the first time. Besides the invasive first stage male and female crabs, one other male stage and four other female stages are reported.

2. The first crab stage (male or female) is hard-shelled, relatively flat and hairy with a distinctive brown color and white markings.

3. Subsequent stages are quite different with membranaceous, yielding carapace, slender legs, and more rounded body form.

4. The later stages of the females are distinguished from one another by size, color, width and shape of abdomen with relation to the rest of the body and size and differentiation of the pleopods. Maturity is usually reached in the fifth stage female and ovigerous crabs have been seen.

5. All stages of crabs have been found in oysters either singly or in various combinations except that no more than one specimen of a Stage III, IV, or V female has ever been observed within a single oyster.

6. Multiple infestations have been observed which involve chiefly first stage crabs. One oyster contained 262 of these crabs.

7. The oyster crab feeds chiefly on the particulate food material strained from the water by the oyster's food sorting mechanism.

8. In so feeding the crab injures the demibranchs of the oyster causing erosions which interfere with normal feeding of the oyster. These erosions are sharply localized in oysters with first stage crabs.

9. Damage to the oyster gills involves a reduction in the amount of area available for food collecting and in the efficiency of both the straining and the collecting mechanisms. The more serious lesions may also show leakages of the water pumping or conduction system which is such an important feature of food sorting.

10. Rapid healing and regeneration of gill tissue almost keeps pace with destruction and probably saves many oysters from death.

11. The hard shelled, almost tick-like, invasive first stage crabs are less adapted to life within the oyster than the modified later stages. The latter are more resistant to their host's exposure to unfavorable environmental conditions such as storage out of water.

12. Experimental invasion of oysters by crabs has been accomplished but artificial duplication of typical, extensive gill lesions has not yet been obtained.

13. The unprecedented invasion of oysters in 1941 was followed by a lesser invasion in 1942 and probably will follow the usual course of population cycles in future years.

14. The parasitic nature of the crab's relations with the oyster is outlined and reasons suggested why this previously was not found out.

#### LITERATURE CITED

- ATKINS, D., 1926. The moulting stages of the peacrab (*Pinnotheres pisum*). *J. Marine Biol. Assoc. U. K.*, **14**: 475-493.
- BIRGE, E. A., 1882. On the first zooëa stage of *Pinnotheres ostreum*. *Amer. Nat.*, **16**: 589-591.
- DEAN, BASHFORD, 1892. *Bull. U. S. Fish. Comm.*, **10** for 1890, 351.
- ELSEY, C. R., 1935. On the structure and function of the mantle and gill of *Ostrea gigas* and *O. lurida*. *Trans. Roy. Soc. Canada*, **29** (Sec. 5): 131-158.
- HYMAN, O. W., 1924. Studies on larvae of crabs of the family Pinnotheridae. *Proc. U. S. Nat. Mus.*, **64**: 1-9.
- LEBOUR, M., 1928. Studies of the Plymouth Brachyura. II. The larval stages of *Ebalia* and *Pinnotheres*. *J. Marine Biol. Assoc. U. K.*, **15**: 109-123.
- MERCIER, L., AND R. POISSON, 1929. Alteration de certaines caractères sexuels secondaires du mâle de *Pinnotheres pisum* L. parasité par un Entoniscien (*Pinnotherion vermiforme* Giard et J. Bonnier). *Bull. Soc. Zool. France*, **54**: 301-304.
- NELSON, T. C., 1938. The feeding mechanism of the oyster. *J. Morph.*, **63**: 1-61.
- NELSON, T. C., AND L. A. STAUBER, 1940. Observations on some common polychaetes on New Jersey oyster beds with special reference to *Polydora*. *Anat. Rec.*, **78** (suppl.): 102-103.
- OHSHIMA, H., 1927. A Pycnogon living parasitic in a bivalve. *Bul. Sci. Fakult. Terakultura Kjusu Imp. Univ.*, **2**: 366-379.
- ORTON, J. H., 1920-21. The mode of feeding and sex phenomena in the pea-crab, *P. pisum*. *Nature*, **106**: 533.
- RATHBUN, M. J., 1917. Grapsoid crabs of America. *Bull. U. S. Nat. Mus.*, No. 97.
- RYDER, J. A., 1881. Rept. Maryland Fish Comm. for 1880, 24.
- STAUBER, L. A., 1942. The oyster crab, *Pinnotheres ostreum*, parasitic on the oyster. *Anat. Rec.*, **84** (suppl.): 45-46.
- STAUBER, L. A., 1943. Graphic representation of salinity in a tidal estuary. *J. Marine Res.*, **5**: 165-167.
- SWELLENGREBEL, N. H., 1940. The efficient parasite. *Proc. Third Internat. Congress for Microbiology*, New York City.
- YONGE, C. M., 1926. The structure and physiology of the organs of feeding and digestion in *Ostrea edulis*. *J. Marine Biol. Assoc. U. K.*, **14**: 295-386.